

# A FUNCTIONAL CLASSIFICATION OF THE CORONAL PORES OF REGULAR ECHINOIDS

by ANDREW B. SMITH

**ABSTRACT.** Six morphologically distinct types of ambulacral pore, found in a survey of Recent regular echinoids, are described and correlated with the structure of their tube feet. A functional interpretation of pore structure provides considerable information about the tube foot supported and allows the reconstruction of tube feet from fossil echinoid tests. Morphological information, such as the presence or absence of a septum, the thickness of the stem retractor muscle, the presence or absence of a terminal sucking disc and the size of that disc, can all be inferred from the structure of the ambulacral pores. Ecological interpretations concerning the animal's life style, the energy of the environment, the nature of the substrate, the depth, and the temperature can all be advanced once the form of tube feet can be identified. In Britain all but the simplest coronal tube feet make their appearance during the Jurassic.

THE tube feet of Recent echinoids are known to have a variety of structures and functions. They may be involved in locomotion, adhesion, absorption and digestion, gaseous exchange, excretion, burial, feeding, or simple chemosensory reception. These organs are almost entirely composed of soft tissue and are rarely found preserved in the fossil record. The structure of Recent echinoid tube feet is well documented. Most early workers provided only external descriptions of the podia, but more detailed light microscope work has been carried out by Hamann (1887), Smith (1937), and Nichols (1959*b*; 1959*c*; 1961) showing the complexity of these structures. Generalized discussions on the variation in structure of tube feet are given by Loven (1883), Cuénot (1948), Hyman (1955), Durham (1966), and Nichols (1968), while a much fuller and more systematic study of tube feet and ampullae has been carried out by Fenner (1973). In addition to these light microscopy studies, more details on the fine structure of tube feet have been provided by transmission electron microscopy (T.E.M.). These include studies on the sucker (Coleman 1969), tube foot wall (Kawaguti 1964), epidermis (Kawaguti and Kamishima 1964), and ampulla (Kawaguti 1965) of echinoids and on the smooth muscle of tube feet (Dolder 1972) and on muscle attachment (Uhlmann 1968) in other echinoderms.

Tube feet are external extensions of the water vascular system, and each tube foot is connected with an internal ampulla by either one or two pores which pass through the ambulacral plates. On the outer surface of the test there is an area surrounding the pores which is modified to support the tube foot. The structure of this, the periporal area, reflects the structure and function of the tube foot supported. Although the variation in the structure of echinoid tube feet is widely recognized, the corresponding variation in ambulacral pore morphology has largely been ignored. The accurate drawings of Lovén (1883) provided the first detailed record of ambulacral pore structure and its variation, though no explanations or interpretations were given. Nichols (1959*a*; 1959*b*; 1961), as well as providing histological details of the tube feet of *Echinocardium*, *Echinus*, and *Cidaris*, also illustrated the pore structure associated with each tube foot type and pointed out that the structure of ambulacral pores might

provide information about the morphology of tube feet in fossil echinoids. In one paper (Nichols, 1959a) he uses the ambulacral pore structure in interpreting the structure and function of tube feet of the Cretaceous heart urchin *Micraster*, though insufficient information was available on Recent species at that time to allow accurate reconstruction. Smith (1978) has recently used the pore structure of two Jurassic irregular echinoids in reconstructing their tube feet and interpreting their life style. Bonnet (1926) has detailed the structure of the ambulacral pores as they pass through the plate.

The aim of this paper is to provide accurate details of the structure of the ambulacral pores of Recent echinoids and to correlate pore morphology with the structure of the tube foot supported. The functional and ecological inferences which may be drawn from various morphological features will also be discussed.

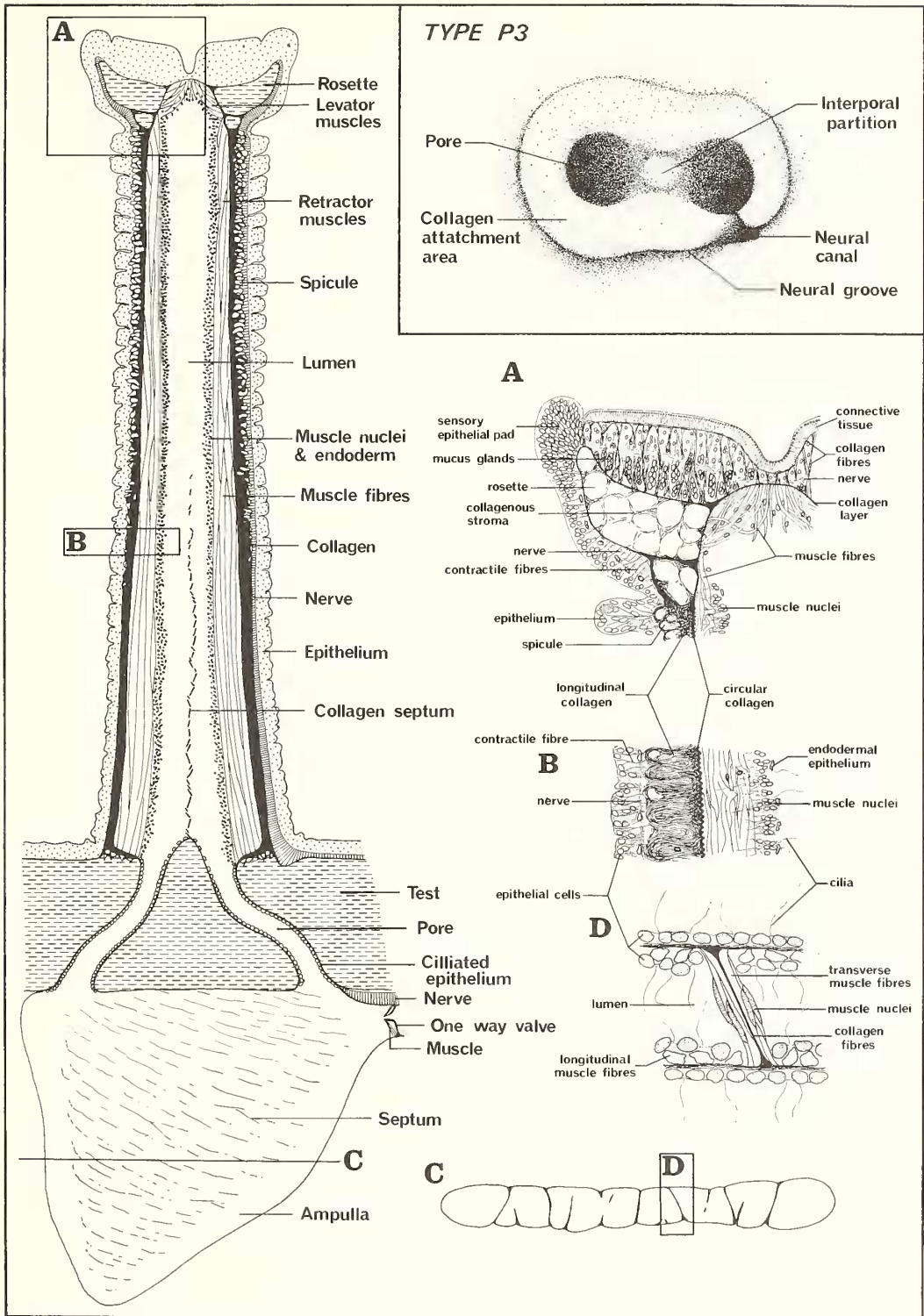
#### MATERIALS AND METHODS

Recent echinoids from as many different families and from as many different habitats as possible were examined and a list of species examined, along with details of their habitat, is given in the Appendix. The histology of oral, ambital and aboral tube feet and ampullae of a large number of species was examined. Animals, if not already preserved, were fixed in a 25% aqueous gluteraldehyde solution. Small pieces of ambulacral column were cut out using a dentist's drill and decalcified in a 10% solution of E.D.T.A. neutralized to a pH of about 7 with NaOH. Decalcification took between one and ten days depending upon the thickness of the test. Specimens were then carefully washed in running water for thirty minutes, dehydrated and embedded in paraffin wax. Serial sections, of between 6  $\mu\text{m}$  and 10  $\mu\text{m}$  thickness, were cut using a microtome and were then stained using the Modified Masson's Technique (see Humason 1972) but substituting two minutes in Aniline Blue for the recommended ten seconds or so in Light Green.

Small pieces of ambulacral column were also removed and placed in a 20% solution of NaOCl for about thirty minutes in order to digest away organic tissue. These cleaned pieces of test were washed in water, dried, and then coated in gold using the Polaron E5000 splatter coater. They were then attached to stubs and placed in a scanning electron microscope (S.E.M.). In addition the pore structure of a number of other Recent echinoids was examined using a high-powered binocular microscope. The ambulacral pores of fossil echinoids were also examined using the S.E.M.

#### STRUCTURE OF CORONAL PORES AND TUBE FEET

A typical tube foot, as described in detail by Nichols (1961), consists of a long cylindrical tube terminating in a sucking disc (see text-fig. 1). This sucker has a two-part skeletal framework, an upper rosette, and a lower frame, both composed of four identical elements. The podial wall consists of a number of layers (text-fig. 1B). Externally there is an epidermal layer with a sub-epidermal nerve plexus, of varying thickness, at its base. Internal to this lies a connective tissue layer which T.E.M. work has shown to be composed of collagen fibres (Kawaguti 1964). This can be subdivided into an outer mass of longitudinally running fibres, which may incorporate spicules



TEXT-FIG. 1. Longitudinal section of an oral tube foot of *Stomopneustes variolaris* (P3 type). Inset shows P3 isopore associated with this tube foot.



especially in the upper part of the stem, and a thin inner layer of circularly running fibres, which may give rise to a septum in the lower part of the tube foot. A third series of fibres lying external to the longitudinal fibres and running circularly is present in very few tube feet. Longitudinal retractor muscle fibres lie internal to the connective tissue layer and their nuclei are found towards the lumen of the podium. A thin layer of epidermal cells, lying amongst the nuclei, lines the lumen.

The connective-tissue layer of the tube foot inserts into the test. Collagen fibres penetrate a short distance into the stereom and are bound round the skeletal trabeculae in the manner described by Nichols and Currey (1968). Penetration is, at the most, only down to the second trabecular layer and, for the most part, fibres are only fastened round the surface trabecular layer. This close association of collagen fibres and trabeculae in the attachment area imparts a distinctive stereom lattice structure which can be readily identified in most genera (Pl. 83, fig. 1; text-fig. 1). The interporal partition, which separates the two pores, may have a variety of shapes (text-fig. 2; text-fig. 3). This interporal area, where it lies within the tube foot lumen, is covered with a single layer of squamous to cuboidal epithelial cells bearing cilia. The septum, where present, runs along the mid-line of the interporal partition, joining the partition's epithelial layer but not actually penetrating into the stereom. The pore lining consists of a basal, very thin, connective-tissue membrane, which may or may not have fine muscle fibres closely associated with it, overlain by densely packed cuboidal epithelial cells with horseshoe-shaped nuclei and with many cilia. The adradial pore bears a groove, termed the neural canal, which is never completely isolated from the pore and always abuts on to the adoral plate suture. This houses a branch of the radial nerve which splits into two parts externally, one running straight up the tube foot from the neural canal, the other linking with the subepidermal nerve plexus of the plate surface. The neural groove associated with the neural canal marks the main passageway of this nerve and may be quite extensive. Internally the pores diverge (see Bonnet (1928) for details) and open into the ampulla, a flattened thin-walled structure (text-fig. 1C, D). There is a one-way valve controlling the flow of coelomic fluid to and from the radial water canal. This consists of a wedge of connective tissue blocking the branch of the radial water canal save for a narrow central slit with abradially directed lips. Muscle fibres run from the lips of the valve to the wall and, upon contraction, will hold the passageway open.

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#### EXPLANATION OF PLATE 81

S.E.M. photomicrographs of echinoid ambulacral pores. Top of photomicrograph adapical.

Fig. 1. *Phormosoma placenta*; aboral P1 isopore.

Fig. 2. *Calveriosoma hystrix*; aboral P1 isopore.

Fig. 3. *Salenocidaris profundus*; aboral P1 isopore.

Fig. 4. *Austrocidaris canaliculata*; aboral P1 isopore.

Fig. 5. *Centrostephanus nitidus*; aboral P1 isopore.

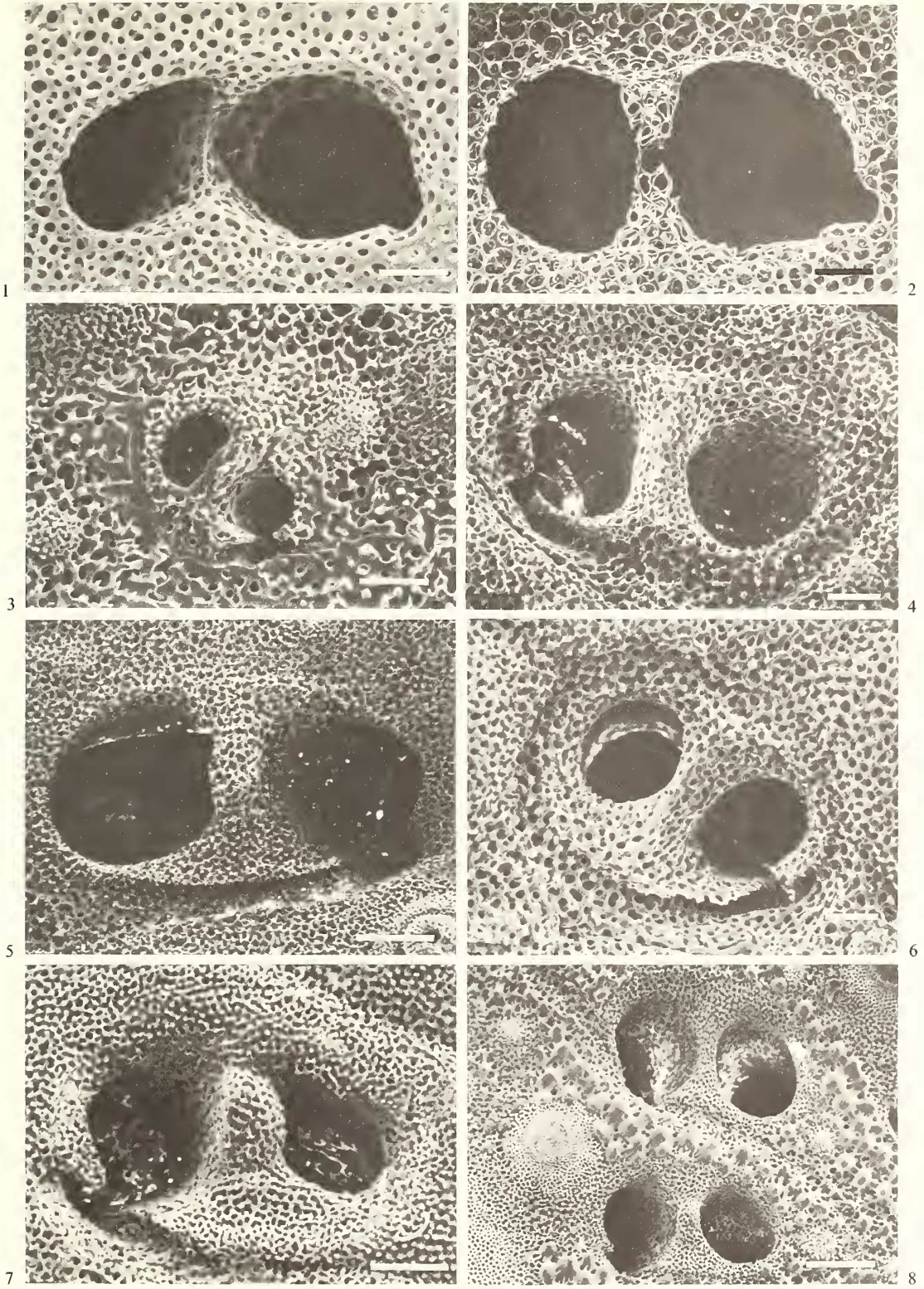
Fig. 6. *Austrocidaris canaliculata*; oral P2 isopore.

Fig. 7. *Echinus acutus*; oral P2 isopore.

Fig. 8. *Sphaerechinus granularis*; aboral P2 isopores.

Scale bar: 1, 2, 3, 4, 6, 8 = 100  $\mu\text{m}$ ; 5, 7 = 200  $\mu\text{m}$ .





ANDREW B. SMITH, Functional classification of echinoid ambulacral pores. I.

All coronal pore structures of regular echinoids possess two more or less equal-sized pores per tube foot. These are therefore termed *isopores* to distinguish them from structures where the two pores are markedly unequal in size (*anisopores*) or where only a single pore penetrates the test (*unipores*). Further subdivision of coronal isopores is made on the presence or absence of a conjugate groove giving two categories of isopores: partitioned and conjugate.

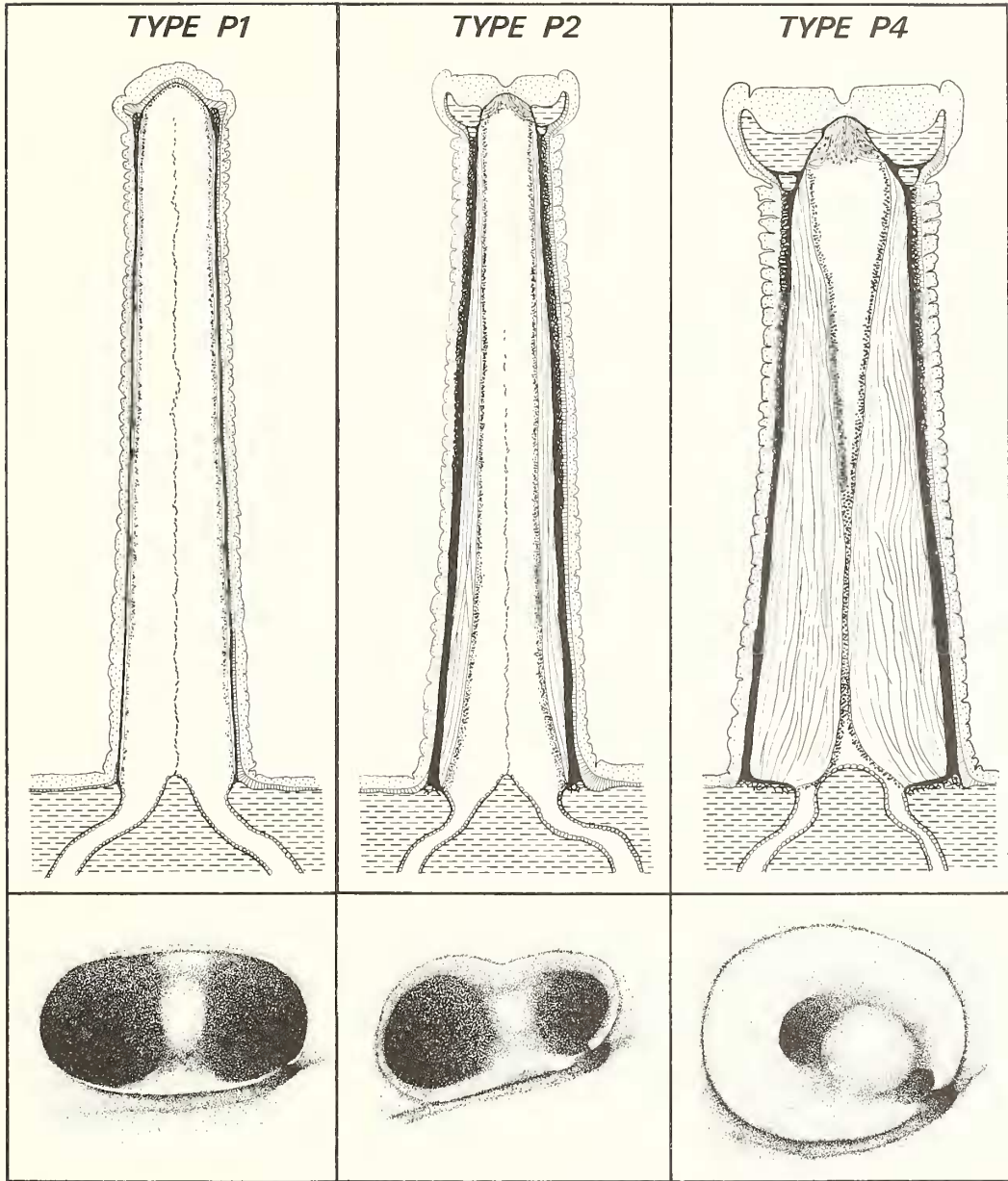
*Partitioned isopores.* These possess two approximately equal-sized pores, the perradial one of which bears a small neural canal. They are oval to circular in outline and possess an interporal partition which is commonly ridged or domed. Four types of partitioned isopores, here designated by the symbol P, can be differentiated on the basis of attachment area breadth, pore size, and interporal partition shape.

*P1 isopores* (Pl. 81, figs. 1–5; text-fig. 2). These are distinguished by the poor development of an attachment area around the pores. There are two types of P1 isopores; small, rounded isopores with a continuous but narrow attachment area, and larger, more elongate isopores with a less clearly defined attachment area. The small subcircular isopores of cidarids and salenioids possess a sharp but narrow attachment area broken only by the neural canal (Pl. 81, figs. 3, 4). The attachment area consists of a row of one or two trabeculae raised above the level of the rest of the stereom and always has a breadth of less than about 25  $\mu\text{m}$ . The interporal partition is narrow and commonly ridged. The pores are quite small. In larger and more elongate isopores the attachment area is well defined only above and below the interporal partition and is lacking laterally (Pl. 81, fig. 5). The isopores of echinothurioids may lack any sign of a specialized attachment area whatsoever (Pl. 81, figs. 1, 2).

The tube feet associated with P1 isopores lack suckers and are thin-walled (text-fig. 2). The apex of the tube foot lacks any skeletal framework and is developed into a small sensory pad. The connective-tissue layer of the stem is very thin and spicules are never common, though vertical rows of single spicules may be associated with the septum. Muscle fibres are small and sparse and form a single layer closely associated with the connective-tissue layer. A septum is always well developed. Slight differences in the structure of the tube foot are found accompanying the differences observed in the isopores. The large isopores with the discontinuous attachment area have very long flattened tube feet. These possess a central septum which runs almost to the apex of the lumen. The apical sensory pad is poorly developed and the connective tissue and muscle layers are extremely thin, their combined thickness being only 1  $\mu\text{m}$  to 3  $\mu\text{m}$ . The connective-tissue layer has only circular-running fibres. The small rounded isopores, on the other hand, support slightly thicker-walled tube feet with both circular and longitudinal connective-tissue fibres. The thickness of the connective tissue and muscle layers combined is about 5  $\mu\text{m}$  to 10  $\mu\text{m}$ . The septum is not quite as extensive, reaching about three quarters of the way up the tube foot lumen. A terminal sensory pad is always developed.

*P2 isopores* (Pl. 81, figs. 7, 8; Pl. 82, figs. 1–8; text-fig. 2). An attachment area, continuous except for the neural canal, is present in P2 isopores. It may be quite distinct (Pl. 82, fig. 1) or may be very difficult to make out (Pl. 82, fig. 2). The pores tend to be moderately large and form a major part of the isopore. The attachment





TEXT-FIG. 2. Longitudinal sections of the tube feet of *Centrostephanus nitidus* (P1 type), *Echinus esculentus* (aboral P2 type), and *Arbacia lixula* (P4 type). Associated isopores are illustrated beneath each tube foot. Stippling as in text-fig. 1.



area has a variable breadth of between 30  $\mu\text{m}$  and 80  $\mu\text{m}$  though in places it may be narrower. The interporal partition is usually arched (Pl. 82, fig. 8).

The tube foot associated with P2 isopores possesses a small terminal sucker with a diameter of between 300  $\mu\text{m}$  and 600  $\mu\text{m}$ . The morphology of this terminal sucking disc is similar to that shown in text-fig. 1A. The connective-tissue layer, with both circular and longitudinal fibres, is moderately well developed in the stem and has a thickness of between 7  $\mu\text{m}$  and 25  $\mu\text{m}$ . Levator muscles, as well as retractor muscles, are present. The thickness of the retractor muscle-fibre layer varies along the length of the stem but is never more than a few fibres thick. These muscle fibres attach to the connective-tissue layer of the tube foot immediately above where this inserts into the stereom. A septum is present and extends between one-third and two-thirds of the length of the tube foot lumen.

P3 isopores (Pl. 83, figs. 1-4; text-fig. 1). Pores are relatively smaller and are rounded. They are surrounded by a broad attachment area continuous except for the neural canal. The attachment area is readily identifiable and has a breadth of between 100  $\mu\text{m}$  and 200  $\mu\text{m}$  though in small isopores it might be slightly narrower. In small P3 isopores the maximum breadth of the attachment area, measured between the pore and the periphery, is always greater than the pore diameter. The interporal partition may be reduced to a small knob by encroachment of the attachment area (Pl. 83, fig. 3) or may be narrow and convex if the isopore is large (Pl. 83, fig. 1). The isopore usually has a subcircular outline.

P3 isopores support tube feet with terminal sucking discs (text-fig. 1A). The diameter of these discs depends primarily upon the diameter of the stem and is found in most cases to lie between 700  $\mu\text{m}$  and 900  $\mu\text{m}$ . The stem has a well-developed connective-tissue layer between 10  $\mu\text{m}$  and 60  $\mu\text{m}$  in thickness and a thick retractor muscle-fibre layer which varies in thickness along the length of the stem. The connective tissue inserts into the outer margin of the attachment area and a thin layer also extends inwards over the whole of the attachment area. This layer penetrates the stereom and is bound round the surface trabeculae. The retractor muscle fibres attach on to this basal connective-tissue layer. This insertion may well be similar to that described by Uhlmann (1968) for muscle attachment in asteroids. A septum is present in these tube feet. Where the interporal partition is long and relatively narrow, this septum

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#### EXPLANATION OF PLATE 82

S.E.M. photomicrographs of echinoid ambulacral pores. Top of photomicrograph adapical unless otherwise indicated.

Fig. 1. *Psammechinus miliaris*; aboral P2 isopore.

Fig. 2. *Tripneustes gratilla*; ambital P2 isopore.

Fig. 3. *Echinus esculentus*; aboral P2 isopore.

Fig. 4. *Centrostephanus longispinus*; sub-ambital P1/P2 intermediate isopore.

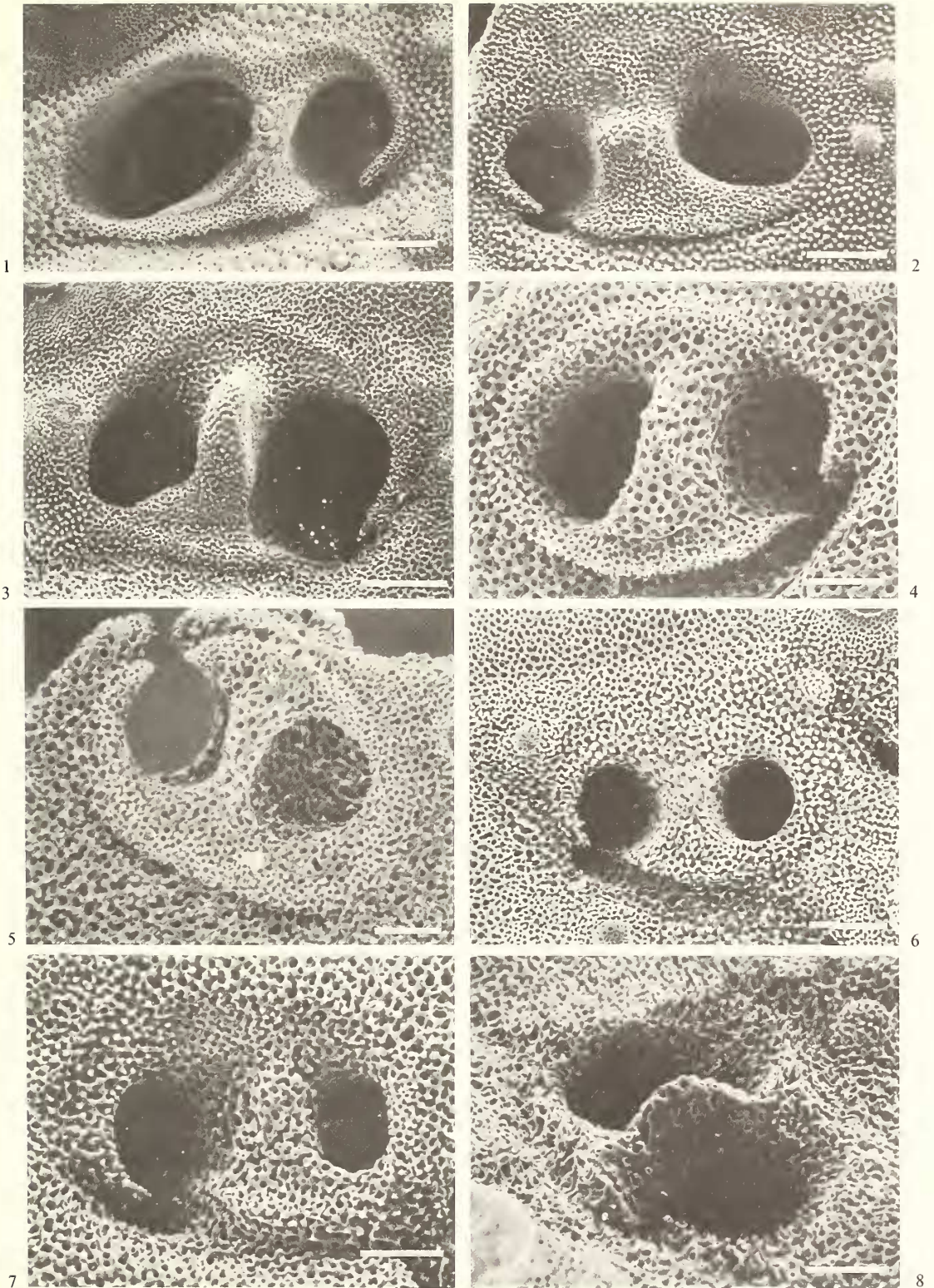
Fig. 5. *C. nitidus*; oral P2 isopore. Top of photomicrograph adoral.

Fig. 6. *Echinostrephus molaris*; adoral P2 isopore.

Fig. 7. *Temnopleurus hardwicki*; oral P2 isopore.

Fig. 8. *Stomopneustes variolaris*; aboral P2 isopore, side view. Adoral to the left.

Scale bar: 1, 2, 3 = 200  $\mu\text{m}$ ; 4, 5, 6, 7, 8 = 100  $\mu\text{m}$ .



ANDREW B. SMITH, Functional classification of echinoid ambulacral pores. I.



usually extends to about one-third of the length of the lumen but where an interporal knob is developed the septum is shorter.

*P4 isopores* (Pl. 83, figs. 5, 6; Pl. 84, figs. 1, 2, 6; text-fig. 2). Both pores are small and are separated by a large interporal partition. The attachment area is very broad, being greater than 200  $\mu\text{m}$  in breadth around most of its length. The isopore is more or less circular in outline and quite distinctive.

The associated tube foot bears a large and well-developed terminal sucking disc closely similar to that present in P3-type tube feet (text-fig. 1A) but larger in diameter. For example the diameter of the terminal sucker is between 1000  $\mu\text{m}$  and 1200  $\mu\text{m}$  in *Arbacia* specimens. A connective-tissue layer is well developed in the stem and has a thickness of about 20  $\mu\text{m}$  to 30  $\mu\text{m}$ . The retractor muscles are developed to such an extent that the lower one-third of the tube foot appears when contracted to have no lumen. These muscle fibres attach on to the stereom via a connective-tissue basal layer, as described previously. A septum is completely lacking and the bulbous interporal partition is covered with a single layer of ciliated epithelial cells.

These four categories of partitioned isopores are readily recognizable but define arbitrary regions in a continuum. There is a complete series of isopores from those having no attachment area to those with an attachment area of considerable breadth. Intermediates are often encountered and it may be impossible to assign such isopores to any one type with certainty. A corresponding variation in tube foot morphology is likewise found. It is quite common to find intermediate tube feet at the ambitus. For example *Centrostephanus rogersi* displays a complete range of tube feet and isopores from P1-type aborally to P3-type around the peristome with P2-type just below the ambitus. The delineation of these four categories does, however, provide a framework into which many isopores may be placed.

*Conjugate isopores*. Like regular isopores, these possess two approximately equal-sized pores, the perradial one of which bears a small neural canal. These circular pores are separated by a broad interporal area which is usually at least equal in breadth to the diameter of the pores. In most cases the two pores are linked by a depression, narrowest centrally and broadening towards each pore. This is the interporal furrow. The stereom of the interporal area outside the interporal furrow differs from that found in partitioned isopores. In conjugate isopores the trabecular intersections have pronounced thorns, whereas in partitioned isopores the stereom of the

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#### EXPLANATION OF PLATE 83

S.E.M. photomicrographs of echinoid ambulacral pores. Top of micrograph adapical.

Fig. 1. *Echinus esculentus*; sub-ambital P3 isopore.

Fig. 2. *Paracentrotus lividus*; ambital P3 isopore.

Fig. 3. *Stomopneustes variolaris*; oral P3 isopore.

Fig. 4. *Echinometra mathaei*; oral P3 isopores.

Fig. 5. *Arbacia lixula*; oral P4 isopore.

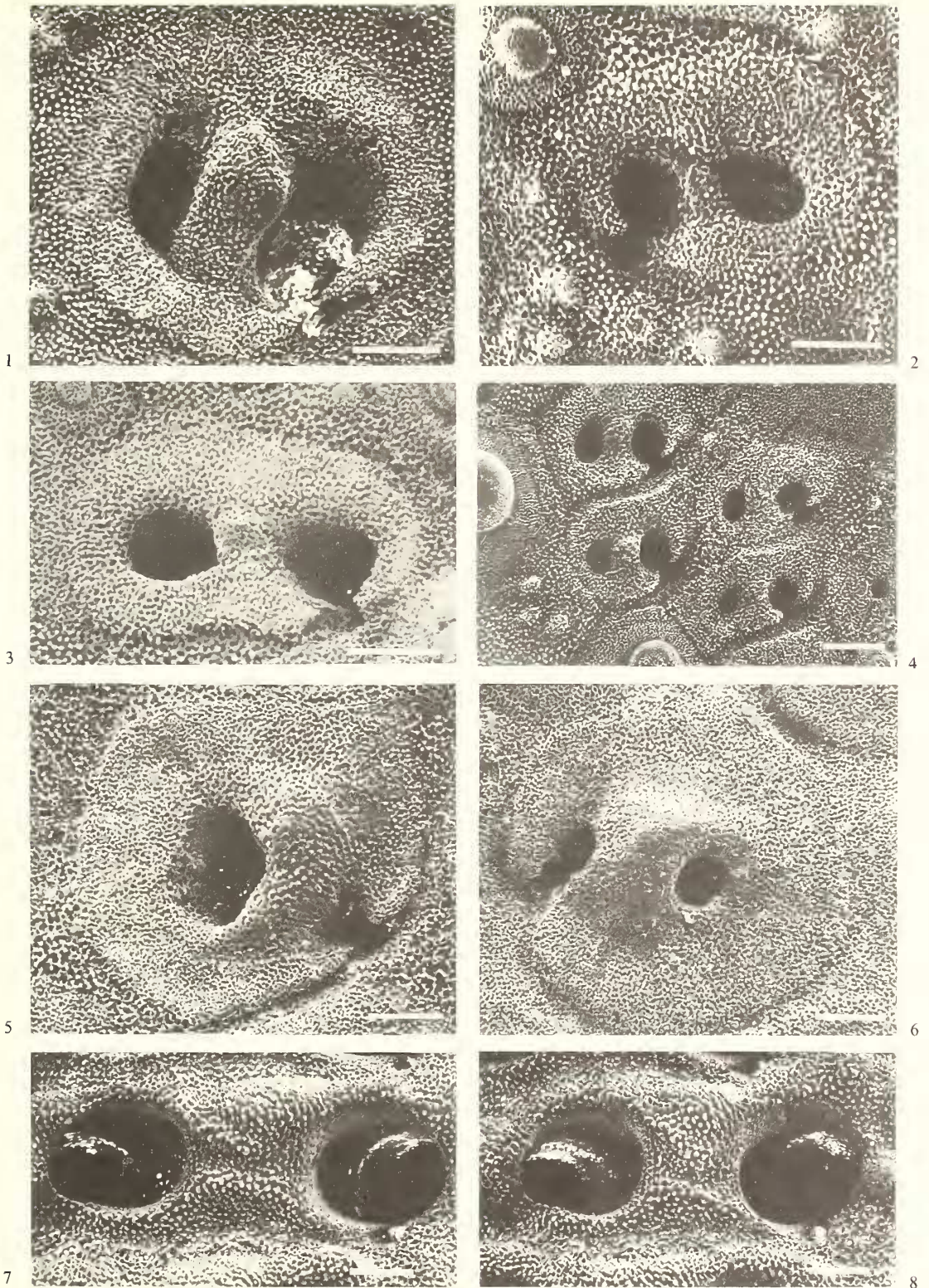
Fig. 6. *Colobocentrotus atratus*; oral P4 isopore.

Fig. 7. *Arbacia lixula*; aboral C1 isopore.

Fig. 8. *A. punctulata*; aboral C1 isopore.

Scale bar = 200  $\mu\text{m}$ .





ANDREW B. SMITH, Functional classification of echinoid ambulacral pores. I.



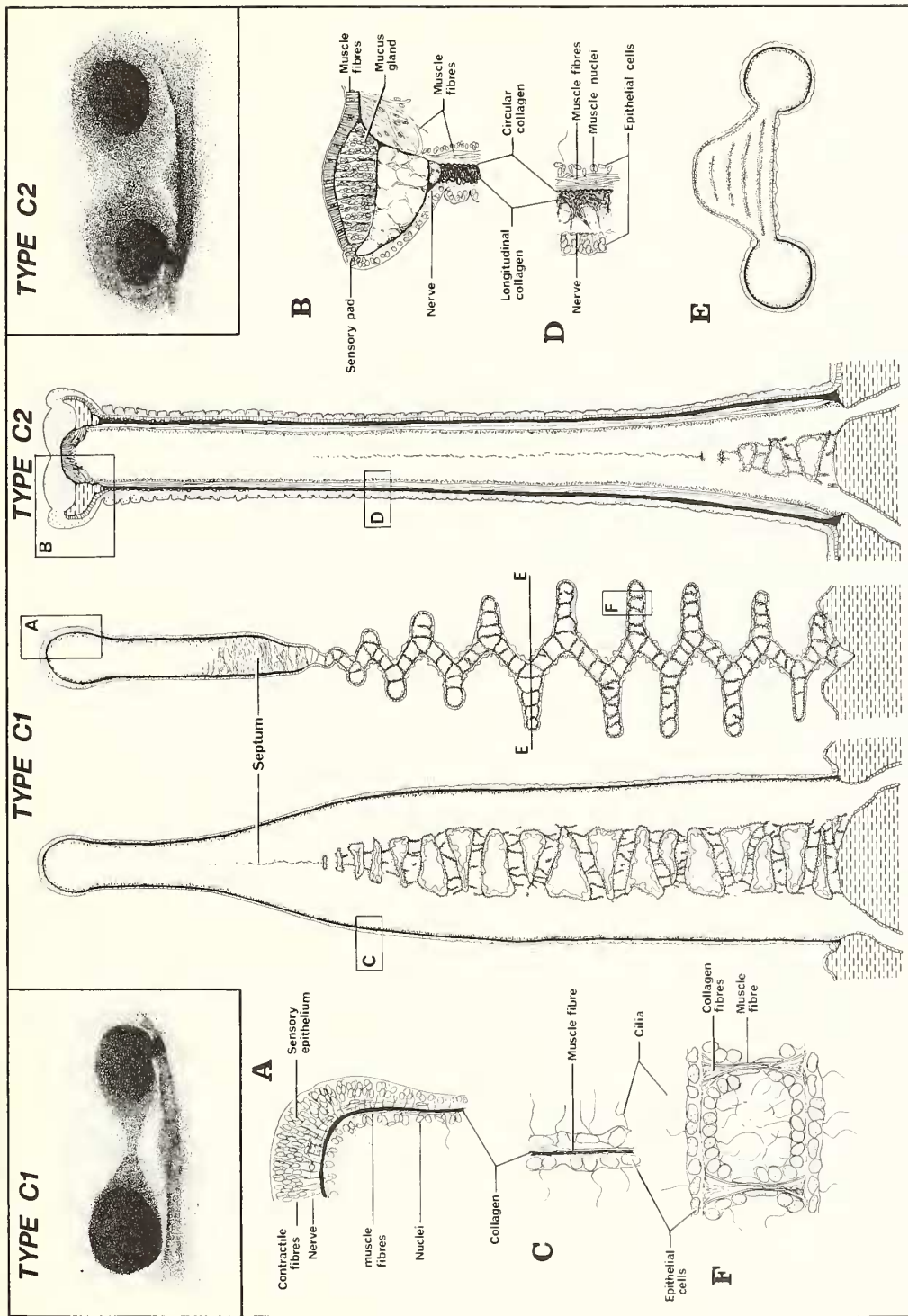
interporal partition is smooth and lacks thorns completely. Raised granules are usually found surrounding the periporal area. Conjugate isopores, here designated by the symbol C, are separated into two categories based on the presence or absence of an attachment area. These are the end members of a continuous series.

*C1 isopores* (Pl. 83, figs. 7, 8; Pl. 84, figs. 4, 5, 7; text-fig. 3). The isopore is large and elongate and both pores are large and circular. The neural canal is small and may be poorly defined. An attachment area is lacking except marginal to the neural canal, where a very thin ridge, less than 25  $\mu\text{m}$  broad may be encountered. The interporal area is broad and often has one or two granules on it. The interporal furrow may or may not be well defined and is relatively narrow. Although in most cases this furrow crosses the interporal area centrally, it may be displaced (Pl. 84, figs. 4, 5) or even absent altogether.

The associated tube foot has a rather complex structure (text-fig. 3). It is composed of two thin-walled cylinders, which merge towards the apex, and a central convoluted area. This central region is very thin-walled and has many septa. The entire lumen is endowed with an epithelial lining rich in cilia and the coelomic fluid is channelled from one cylinder to the other through this central region. In *Eucidaris* this convoluted area has lobe extensions at each bend (text-fig. 3F) which greatly increase its surface area. However these lobes are lacking in *Arbacia* spp., as is the small development of septum present above the convoluted area. Muscle fibres are present but are small and sparsely distributed. They are closely associated with the very thin circular connective-tissue layer and the combined thickness of these two layers is only about 2  $\mu\text{m}$ . The apex of the tube foot terminates in a poorly developed sensory pad (text-fig. 3A) with a slightly thickened nerve plexus underlying dense epithelial tissue. The connective-tissue layer does not penetrate into the stereom of the test but merges with the basal membrane of the pore lining. The base of the central rippled area attaches to the walls of the interporal furrow but again no penetration of the stereom is found. A short septum may or may not be present above the rippled area.

*C2 isopores* (Pl. 84, fig. 3; text-fig. 3). These are less elongate than C1 isopores and possess smaller circular pores, the periradial of which bears a well-defined neural canal. These pores are separated by a broad interporal region which possesses a rather broad and poorly defined interporal furrow linking the two pores. Surrounding each pore there is a recognizable attachment area of moderate breadth which slopes inwards.

The tube foot supported by C2 isopores has a small terminal sucker, about 350  $\mu\text{m}$  in diameter in *Eucidaris*, with the same basic construction as P-type suckered tube feet (text-fig. 3B). The peripheral sensory pad, however, is only poorly developed and the region lying immediately beneath the sucker's cuticle is composed of small muscle fibres running from the connective tissue layer to the cuticle. The detailed histology of a similar suckered tube foot of a cidarid is given by Nichols (1961). It is unlikely to have come from *Cidaris cidaris*, as is stated, as *Cidaris* has non-conjugate isopores and has P-type sucking discs. The tube foot stem of a C2-type tube foot is relatively thick with both circular and longitudinal connective-tissue fibres, about 15  $\mu\text{m}$  to 20  $\mu\text{m}$  in thickness, and with a moderate development of retractor muscle fibres, about 10  $\mu\text{m}$  to 15  $\mu\text{m}$  in thickness (text-fig. 3D). These muscle fibres attach on to the stem connective-tissue layer and not directly on to the test via a basal



TEXT-FIG. 3. Sections through the conjugate tube feet of *Eucidaris metularia*. Left hand diagram; longitudinal section through aboral C1 type tube foot. Central diagram; sagittal section through same tube foot. Right hand diagram; longitudinal section through oral C2 type tube foot. Insets show C1 and C2 isopores associated with these tube feet. Stippling as in text-fig. 1.



connective-tissue layer. The lowest part of the tube foot is expanded and a central convoluted area is found linking the two cylinders, as described for C1-type tube feet.

Conjugate isopores form a continuous series and it is quite possible to find examples of echinoids bearing C1 isopores and tube feet aborally, C2 isopores and tube feet orally and P2 isopores and tube feet around the peristome with all the linking intermediates.

*The umbrella tube feet of Micropyga.* *Micropyga tuberculata* Agassiz bears two types of tube feet aborally: an inner series of simple, thin-walled tube feet with a sensory and respiratory function and an outer series of very long, specialized umbrella tube feet described by Döderlein (1906) and Mortensen (1940a). These umbrella tube feet attach to P2 isopores. This demonstrates that only a limited amount of information is contained in the structure of the isopore and that in some cases more than one type of tube foot may be associated with a particular pore structure.

#### FUNCTIONAL INTERPRETATION OF PORE STRUCTURES

With the exception of the umbrella tube feet of *Micropyga*, noted above, it is possible to recognize or reconstruct the morphology of the tube foot from the structure of the pore to which it attaches. Interpretation of periporal structures can give an insight into the structure and function of the tube feet of fossil echinoids.

*The shape of the isopore.* The presence of two equal-sized pores penetrating through the test permits a one-way current flow of the coelomic fluids (see Fenner (1973) for details). This is important in promoting efficient gaseous exchange by ensuring a separation of oxygenated and deoxygenated coelomic fluid and permitting the maintenance of continuous circulation. Those tube feet, whose primary function is one of gaseous exchange, are associated with isopores which have relatively extensive pores. Tube feet with an adhesive function, and where a thick connective tissue and muscle fibre layer restricts the ability to carry out gaseous exchange, are associated with isopores with large periporal areas and relatively small pores.

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#### EXPLANATION OF PLATE 84

S.E.M. photomicrographs of echinoid ambulacral pores. Top of micrograph adapical unless otherwise stated.

Fig. 1. *Echinus esculentus*; oral P4 isopores.

Fig. 2. *Paracentrotus lividus*; oral P3 isopore transitional to P4 isopore.

Fig. 3. *Eucidaris metularia*; oral C2 isopore.

Fig. 4. *Arbacia punctulata*; aboral C1 isopores, side view. Note the adorally displaced conjugate furrow in the right hand isopore. Adoral to left.

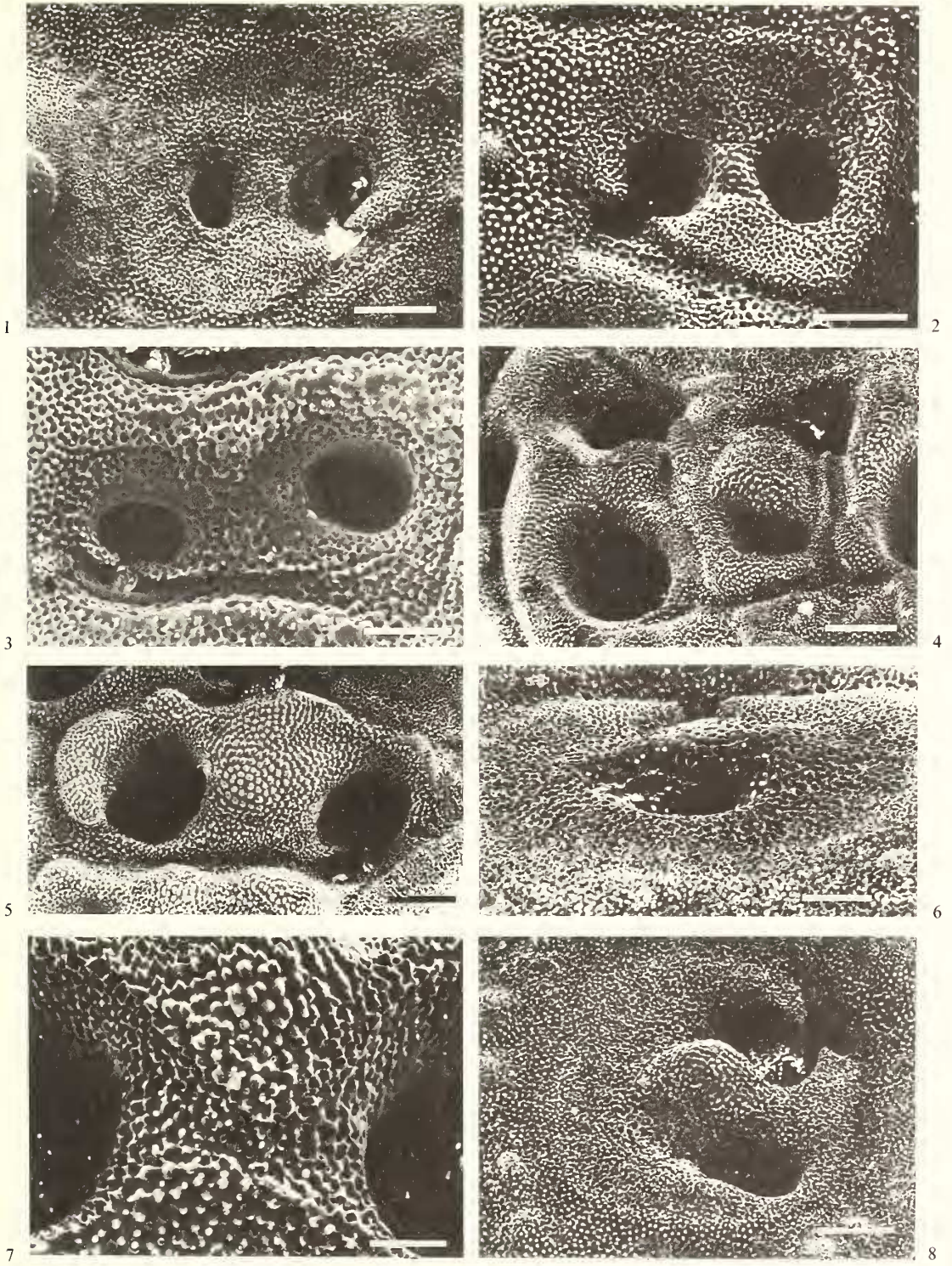
Fig. 5. *A. punctulata*; aboral C1 P3 isopore. Conjugate furrow displaced adorally and not well defined.

Fig. 6. *A. lixula*; oral P4 isopore, side view. Adoral to right.

Fig. 7. *A. lixula*; aboral C1 isopore. Detail of interporal area showing conjugate furrow.

Fig. 8. *Echinus esculentus*; sub-ambital P3 isopore, side view. Adoral to right.

Scale bar: 1, 2, 4, 5, 8 = 200  $\mu\text{m}$ ; 3, 6, 7 = 100  $\mu\text{m}$ .



ANDREW B. SMITH, Functional classification of echinoid ambulacral pores. I.



The degree of divergence of the pores while passing through the test also reflects the emphasis placed upon gaseous exchange in the tube foot/ampulla system. Pores which diverge markedly and open widely separated into the interior of the test have long, flattened, thin-walled ampullae crossed by numerous septa. These ampullae are presumably respiratory in function. The connective-tissue layer of these ampullae is only  $1\ \mu\text{m}$  to  $3\ \mu\text{m}$  in breadth. A reduction in the respiratory function of the system is accompanied by a reduction in the degree of pore divergence. The ampullae associated with weakly divergent pores are much narrower and usually somewhat broader, with a tendency to become cylindrical tubes towards their free end. The ampulla walls have a slightly thickened connective-tissue and muscle-fibre layer, about  $4\ \mu\text{m}$  to  $8\ \mu\text{m}$  in total.

The outline of the isopore can vary from being very elongate to being more or less round. This is related to the function of the tube foot supported. Where gaseous exchange is the main function of the tube foot, then a large ratio of surface area to volume is required. This is achieved by a flattening of the tube foot along the axis joining the two pores. Where the tube foot is primarily concerned with adhesion, then the ratio of surface area to volume becomes unimportant whereas the area of attachment becomes more critical. For mechanical reasons it is advantageous for the stem to splay out slightly towards its base so that the contracted tube foot is more capable of compensating for lateral forces. These adhesive tube feet have a base of approximately the same maximum diameter as that of the terminal disc, and the more important the tube foot is for attachment, the rounder is the periporal area.

*Size of the attachment area.* The area for collagen attachment has stereom of distinctive lattice structure and may also be slightly raised above the rest of the test. In some species however, where the attachment area is small, it may be difficult to identify without the use of an S.E.M. (Pl. 82, fig. 2). The size of the attachment area provides information on the quantity of stem muscle fibres developed. These muscles function in retracting the tube foot and are well developed only where adhesion is important. Tube feet with weak sucking discs or simple sensory pads require few retractor muscle fibres and these attach to the connective tissue layer at its base. Where a large and powerful terminal sucking disc is present, then the number of retractor muscle fibres required to affix the animal securely in a high energy environment is greater, and the muscle fibres attach via a connective-tissue membrane on to the periporal area. The breadth of the attachment area gives direct information on the thickness of the retractor muscle layer in the stem of the tube foot supported.

*Shape and size of the interporal partition.* Where the interporal partition forms a fairly well-defined ridge, then the associated tube foot always appears to be endowed with a large septum. In P1 and P2 tube feet the septum is long, extending at least three-quarters of the length of the tube foot. P3 tube feet have shorter septa, about a third to a half of the length of the tube foot, while P4 tube feet completely lack any septum. The development of the central septum can be correlated with the function of the tube foot. Where gaseous exchange is the principal function of the tube foot, it is important to have as large a surface area as possible. In respiratory tube feet this is assisted by the septum which ensures that the coelomic fluid follows the longest path



from one pore to the other, optimizing the efficiency of gaseous exchange in a cylindrical system.

With a decrease in the respiratory function of the tube foot, the septum becomes less important and may be lost altogether. The collagen and muscle layers provide a barrier against diffusion of gases. In P1 tube feet the total thickness of these layers is around 1  $\mu\text{m}$  to 5  $\mu\text{m}$ , whereas in P4 tube feet the total thickness of these layers varies between 50  $\mu\text{m}$  and 350  $\mu\text{m}$ . Gaseous exchange across these thicker walls must be fairly minimal and unimportant. Where no septum is present the interporal partition is developed into a bulbous dome, covered in life with a single layer of ciliated epithelial cells. This ensures that movement of the coelomic fluid is maintained within the lumen of the tube foot even when the tube foot is at rest. The interporal partition has nothing to do with muscle attachment as postulated by Nichols (1959a).

*Presence of a conjugate furrow.* Where a furrow is present in the interporal area, linking the two pores of an isopore, the associated tube foot has a central rippled area as described above. The interporal furrow delineates the position of this central region (see text-fig. 3). This convolute area greatly increases the surface area of the tube foot and divides the inflowing oxygen-deficient coelomic fluid into many streams. The walls of the tube foot have very thin connective-tissue and muscle layers in C1 forms, and must permit considerable gaseous exchange to occur. As well as increasing the surface area across which gaseous exchange can occur, the central region also acts to separate the inflowing oxygen-poor current from the outflowing oxygen-rich current. In P1 tube feet these two currents are separated only by a thin collagenous septum, and oxygen depletion of the outflowing current must occur by diffusion across the septum. Tube feet with a central convoluted area avoid this problem by the complete separation of the oxygen-rich and oxygen-poor fluids along most of the tube foot's length. Gaseous exchange is therefore probably more efficient in C-type tube feet than in P-type tube feet.

*Neural canal.* The neural canal houses a branch of the radial nerve. In most coronal isopores it is moderately well developed, especially where a terminal sucking disc is supported. The coordination required to operate a sucking disc demands a well-developed tube-foot nerve. Respiratory tube feet have only a small sensory pad at their apex; the tube-foot nerve is small and difficult to find and may even be absent in some (though a thin nerve plexus is always present). The neural branch to the sub-epidermal nerve plexus is always developed, and the neural canal, although small, is not absent altogether from isopores of respiratory tube feet.

#### ECOLOGICAL INTERPRETATION OF PORE STRUCTURES

*Substrate and energy of environment.* The strength of a suckered tube foot is determined by two variables; the tensile strength of the stem and the adhesive power of the terminal sucking disc. The quantity of muscle fibres in the tube-foot stem is thought to determine its tensile strength and, as has already been discussed, the breadth of the attachment area is directly proportional to the amount of stem muscle. There is also evidence that the size of the terminal sucking disc is directly related to its adhesive power (Sharp

and Gray, 1962). The maximum diameter of the pore approximates fairly closely to the diameter of the terminal sucking disc in P2, P3, and P4 isopores. Thus some idea of the adhesive power of the terminal sucking disc can be gained from the structure of the isopore.

The tenacity with which an individual can cling to a surface is determined by the tube foot strength, the number of tube feet which are involved, and the size and shape of the test. These factors affect the distribution of the species and determine the maximum environmental energy that can be withstood. Two series of experiments have been carried out on the clinging ability of echinoids. Sharp and Gray (1962) demonstrated that *Arbacia punctulata* (P4 isopores orally), when subjected to a constant pull of 250 g, had a longer clinging time than *Lytechinus variegatus* (P2 isopores orally), on rocks in an aquarium. Individuals of both species were also transplanted on to a rocky jetty and it was found that, whereas *Arbacia* quite happily colonized this high energy environment, *Lytechinus* individuals were quickly washed away. Sharp and Gray suggest that the greater clinging power of *Arbacia* was due to the large size of the sucker discs of its tube feet (about twice the diameter of the discs of *Lytechinus*) and their thicker and stronger stems.

Markel and Titschack (1965) carried out similar experiments with *Arbacia lixula*, *Paracentrotus lividus*, and *Sphaerechinus granularis* (P4, P3, and P2 isopores orally, respectively) in which a spring balance was used to measure the maximum pull individuals could withstand. They report that the majority of tube feet shear before the terminal sucking disc is detached from the substrate and that the tensile strength of the stem limits the tube foot strength. *Paracentrotus* is reported to be able to withstand a much greater pull than *Arbacia*, despite having weaker individual tube feet, because of the greater number of oral tube feet involved in adhesion.

How meaningful these experimental measurements are is uncertain. The stresses produced by breaking waves, which shallow-water echinoids have to cope with, are short and sharp. The strain induced in tube feet from stress applied over a period of time is likely to differ from that experienced in the natural environment. Although experimental evidence suggests that *Paracentrotus* is better adapted for adhering to rocks in a high energy environment than *Arbacia*, in the natural situation *Arbacia* populations are found at shallower depths or in more exposed situations than *Paracentrotus* populations (Kempf, 1962; Neill and Larkum, 1965). Much more experimental work must be carried out before quantitative information can be considered reliable.

Despite this lack of quantitative information, broad generalizations about the habitat of any species can be drawn purely from a consideration of the pore structure. A list of the types of isopores found in each species examined is given in the Appendix, and this also provides details of the environment in which they live. From this it can be seen that Recent species with oral P1 isopores are uncommon and are found only on soft bottoms in the deep sea environment. Oral P2 isopores are present in species living in all environments from the abyssal to the subtidal, but all are restricted to a low to moderate energy of environment. These species also live on soft or firm sediment bottoms, though some shallow-water species may seek protection in rock crevices or overhangs bounding sedimentary areas. Oral P3 isopores are present in shallow-water species usually confined to the intertidal and shallow subtidal regions,



though occasionally extending into the deeper waters of the continental shelf. These species live on rocks or reef structures. Subtidally they appear to live out in the open on rock surfaces, while intertidally or immediately infratidally they prefer to inhabit burrows or crevices or live sheltered beneath boulders. P4 isopores are found in echinoids inhabiting steep rocky bottoms or coral reefs in exposed high energy environments. They live in the intertidal or immediately subtidal zones on the open surface of rocks, though intertidally they may inhabit crevices.

Although pore structure can only allow broad generalizations to be drawn, it does provide some information useful in the interpretation of the habitats and life styles of fossil echinoids. In attempting to ascertain the clinging power of a fossil echinoid the following factors must be taken into consideration: the breadth of the attachment area (tensile strength of the stem), the maximum diameter of the isopores (size and adhesive power of the terminal sucking disc), the number of oral isopores, and the size of the test. For example both *Echinus esculentus* and *Stomopneustes variolaris* have oral tube feet with similar-sized terminal sucking discs and similar development of stem muscle fibres. *Stomopneustes* however, has very pronounced phyllodes which *Echinus* lacks. *Stomopneustes* is also considerably smaller than *Echinus* and therefore possesses many fewer oral tube feet with which to adhere. However, in relative terms, for its size *Stomopneustes* has more tube feet with larger sucking discs and can therefore colonize high-energy intertidal environments where it lives in crevices. *Echinus*, on the other hand, with proportionally fewer and smaller tube feet for its size, inhabits a slightly lower energy environment in the shallow subtidal region. A small species, with numerically fewer and proportionally larger tube feet is able to adhere in more energetic conditions than a large species.

The presence of phyllodes on the oral surface of regular echinoids has been mentioned by Kier (1974). In uniserial pore arrangements the occurrence of small broadened ambulacral areas of P2 or P3 isopores around the peristome provides increased numbers of suckered tube feet to counteract the stresses of mastication. In echinoids with trigeminate or polyporous ambulacral columns the development of broad oral phyllodes, composed of P3 or P4 isopores, allows firmer attachment to the substrate. They are present in only those species which inhabit exposed high-energy intertidal or immediately subtidal environments. The deep-sea urchin *Phormosoma placenta*, which completely lacks oral suckered tube feet, is unlikely to be able to graze like other regular echinoids. Lawrence (1975) reports that deep sea echinothurioids in fact eat bottom ooze, and it seems likely that echinoids lacking oral suckered tube feet feed primarily by swallowing sediment.

Aboral tube feet are either respiratory in function (C1 and P1 types) or are thin-walled and terminate in a small sucking disc (P2 type). From the available information it appears that regular echinoids with aboral suckered tube feet cover themselves with particles to some degree. There has been much discussion as to the exact cause and purpose of this covering reaction (see Lawrence (1976) for a recent review). It may well be that the covering reaction fulfils different functions in different groups of species.

*Respiration and Temperature.* An echinoid's demand for oxygen depends upon its size, its developmental stage, the ambient temperature and the animal's activity (Farmanfarmanian, 1966). Up to a critical level, the metabolic rate of oxygen

consumption increases with increasing temperature. Therefore echinoids inhabiting shallow warm waters have a greater oxygen consumption than those in colder waters. Echinoids inhabiting shallow tropical waters need the most efficient respiratory tube feet. This is best displayed by recent cidarids where both P1 and C1 tube feet may occur aborally. All those cidarids examined which inhabit shallow-water coral-reef environments, usually at depths of only a few metres, possess C1 tube feet aborally. Cidarids from colder-water shelf areas or from deeper waters where the oxygen consumption rate *per se* is reduced, possess only P1 tube feet aborally.

Non-cidaroid echinoids do not display such a clear correlation between type of tube foot and habitat. Many shallow-water echinoids have found it advantageous to be able to cover themselves. Arbacioids possess only a single row of tube feet aborally in each ambulacral column and their P4 oral tube feet, with their extensive collagen and muscle layers, can play no effective part in gaseous exchange. As these species inhabit shallow warm waters, the aboral tube feet have to be very efficient at gaseous exchange. Arbacioids possess C1 tube feet aborally. Diadematooids also possess only uniserial rows of tube feet aborally and these tube feet are again largely respiratory in function. Trigeminate and polyporous ambulacral arrangements produce a marked increase in the number of aboral tube feet and gaseous exchange across individual tube feet becomes less critical. A multiserial arrangement provides sufficient numbers of aboral tube feet to cater for all the echinoid's oxygen requirements even with less efficient and thicker-walled P2 tube feet (see Steen, 1965). In regular echinoids suckered aboral tube feet are only found in species where more than one row of tube feet per ambulacral column is present. Only holoctypoid and pygasteroid species possess single rows of P2 isopores.

In deeper-water species, the rate of respiration is presumably reduced and the demand for oxygen small. Specialized tube feet are therefore not required. Aboral adhesive suckered tube feet are also redundant in this environment and therefore these species possess P1 aboral tube feet. These tube feet, while meeting the respiratory needs of the animal, fulfil a sensory role and can be distinguished from shallow-water respiratory tube feet by the structure of the isopore. In respiratory P1 tube feet the two ambulacral pores diverge as they pass through the test, whereas in sensory P1 tube feet the pores pass through the test with little or no divergence (Pl. 81, figs. 1, 2) and link with small fairly thick-walled ampullae.

#### FOSSIL CORONAL PORES

In addition to the large number of Recent echinoids studied, considerable numbers of fossil echinoids, ranging from the Ordovician to the Tertiary, were examined using a S.E.M. In many cases preservation was good enough to allow the identification of isoporal attachment areas and permit the reconstruction of the associated tube feet. All were found to conform to the same basic designs of isopores as are found in Recent echinoids with the exception of *Neobothriocidarid* which will be dealt with elsewhere. It is therefore possible to use isopore morphology to identify the type of tube foot of fossil echinoids by direct comparison with Recent echinoids. Most Palaeozoic echinoids possess P1 isopores with non-divergent pores with P2 isopores occurring adorally. It was only with the rapid burst of evolution at the top of the Lias



that other types of coronal isopores make their appearance. This allowed Jurassic regular echinoids to inhabit all the types of marine environment in which their descendants are found today. Aboral P2 isopores are also found for the first time, indicating that some species were capable of a covering reaction (see Smith, 1978). It should now be possible to use the isopore morphology of fossil regular echinoids to provide evidence for both palaeoecological studies and palaeoenvironmental reconstruction.

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APPENDIX  
*Tube feet and habitat of regular echinoids*

Species	1	2	3	Habitat	References
ORDER CIDAROIDA					
FAMILY CIDARIDAE					
<i>Portocidaris purpurata</i>	SH	P2	P1	N. Atlantic. 750-1804 m. <i>Globigerina</i> ooze.	Farran (1913) Mortensen (1928)
<i>Ctenocidaris speciosa</i>	O	P2	P1	Circum-polar antarctic. 75-400 m.	Mortensen (1928)
<i>Austrocidaris canaliculata</i>	SH	P2	P1	Magellanic region. 9-1100 m. Sand; sand and gravel.	H. L. Clark (1925b)
<i>Gontocidaris tubaria</i> var. <i>impressa</i>	O	C2	C1	Australia. Littoral-150 m. Sheltered bay; prefers sandy or grass bottoms.	Mortensen (1928) H. L. Clark (1946) A. M. Clark (1966)
<i>G. biserialis</i>	O	P2	P1	Japan, Korea. 70-500 m. Prefers hard bottoms.	Mortensen (1928)
<i>Phyllacanthus imperialis</i>	O	C2	C1	Indo-W. Pacific. Littoral-73 m. Coral reefs, in lagoon or outside reef subtidally. Hides under coral blocks during the day, mobile at night.	Mortensen (1928) H. L. Clark (1946) A. M. Clark (1966)
<i>Plolocidaris verticillata</i>	O	C2	C1	Indo-W. Pacific. 0-54 m, mostly littoral. Amongst old coral branches and on coral sands.	Mortensen (1927, 1928)
<i>Prionocidaris bispinosa</i>	O	P2	C1	Indo-W. Pacific. 0-50 m, usually shallow. Coral sand and shell sand bottoms primarily.	Mortensen (1927, 1928) H. L. Clark (1925a, 1932, 1938) Gibbs <i>et al.</i> (1976)
<i>P. baculosa</i>	O	C2	C1	Indo-W. Pacific. 0-200 m, usually very shallow. Seaward side of reef, amongst fringe reefs, in <i>Cyniodocaea</i> beds, in crevices in reef and on coral sand bottoms.	Balinsky (1958) James and Pearse (1969) Oxford Univ. (1972) Evans <i>et al.</i> (1973) A. M. Clark (1976)
<i>Cidaris cidaris</i>	SH	P2	P1	Atlantic, Mediterranean. 60-200 m commonest. On all types of sediments.	Koehler (1927) Cherbonnier (1956)

Column 1. O. Test examined with optical microscope. Column 2. Type of oral isopore. Column 3. Type of aboral isopore.

S. Test examined with S.E.M.

H. Tube feet examined histologically.





## APPENDIX

## Tube feet and habitat of regular echinoids

Species	1	2	3	Habitat	References
ORDER CIDAROIDA					
FAMILY CIDARIDAE					
<i>Poriodicaris purpurata</i>	SH	P2	P1	N. Atlantic. 750-1804 m. <i>Globigerina</i> ooze.	Farran (1913) Mortensen (1928)
<i>Ctenodicaris speciosa</i>	O	P2	P1	Circum-polar antarctic. 75-400 m.	Mortensen (1928)
<i>Austrocidaris canaliculata</i>	SH	P2	P1	Magellanic region. 9-1100 m. Sand; sand and gravel.	H. L. Clark (1925b)
<i>Goniocidaris tubaria</i> var. <i>impressa</i>	O	C2	C1	Australia. Littoral-150 m. Sheltered bay; prefers sandy or grass bottoms.	Mortensen (1928) H. L. Clark (1946) A. M. Clark (1966)
<i>G. biserialis</i>	O	P2	P1	Japan, Korea. 70-500 m. Prefers hard bottoms.	Mortensen (1928)
<i>Phyllacanthus imperialis</i>	O	C2	C1	Indo-W. Pacific. Littoral-73 m. Coral reefs, in lagoon or outside reef subtidally. Hides under coral blocks during the day, mobile at night.	Mortensen (1928) H. L. Clark (1946) A. M. Clark (1966)
<i>Plococidaris verticillata</i>	O	C2	C1	Indo-W. Pacific. 0-54 m, mostly littoral. Amongst old coral branches and on coral sands.	Mortensen (1927, 1928)
<i>Prionocidaris bispinosa</i>	O	P2	C1	Indo-W. Pacific. 0-50 m, usually shallow. Coral sand and shell sand bottoms primarily.	Mortensen (1927, 1928) H. L. Clark (1925a, 1932, 1938) Gibbs <i>et al.</i> (1976)
<i>P. baculosa</i>	O	C2	C1	Indo-W. Pacific. 0-200 m, usually very shallow. Seaward side of reef, amongst fringe reefs, in <i>Cymadocea</i> beds, in crevices in reef and on coral sand bottoms.	Balinsky (1958) James and Pearce (1969) Oxford Univ. (1972) Evans <i>et al.</i> (1973) A. M. Clark (1976)
<i>Cidaris cidaris</i>	SH	P2	P1	Atlantic, Mediterranean. 60-200 m commonest. On all types of sediments.	Koehler (1927) Cherbonnier (1956)
Column 1. O. Test examined with optical microscope. S. Test examined with S.E.M. H. Tube feet examined histologically.				Column 2. Type of oral isopore.	Column 3. Type of aboral isopore.

Species	1	2	3	Habitat	References
ORDER CIDAROIDA (cont.)					
FAMILY CIDARIDAE (cont.)					
<i>Eucidaris metularia</i>	SH	C2	C1	Indo-Pacific. Intertidal-570 m, usually very shallow. Amongst reefs, in tidal pools, in lagoons, inner and middle portion of barrier reef. Under masses of coral debris.	Mortensen (1928) Boone (1938) A. H. Clark (1950, 1952)
<i>Stylocidaris affinis</i>	O	P2	P1	Atlantic, Mediterranean. 0-1000 m, commonest 50-200 m. Coralline algae bottoms and on rock and mud bottoms.	Koehler (1927) Mortensen (1928, 1937) Cherbonnier (1956)
ORDER ECHINOTHURIOIDAE					
FAMILY ECHINOTHURIIDAE					
<i>Calvertosoma hystrix</i>	SH	P2	P1	E. Atlantic. 350-1800 m. Ooze or mud bottoms.	Farran (1913) H. L. Clark (1925b) Mortensen (1935) H. L. Clark (1925b) Madsen (1947)
<i>Hygrosoma petersi</i>	O	P2	P1	Atlantic. 200-3275 m. Mud bottom.	H. L. Clark (1923, 1925b) Madsen (1947)
<i>Phormosoma placenta</i>	SH	P1	P1	Atlantic. 215-2500 m. Mud or ooze bottoms.	
ORDER DIADEMATOIDA					
FAMILY DIADEMATIDAE					
<i>Astropyga pulvinata</i>	O	P2	P1	E. Pacific. 5-30 m. Coral reef on sand and rubble bottoms.	Mortensen (1940a) A. M. Clark (1976)
<i>A. radiata</i>	O	P2	P1	Indo-W. Pacific. 2-60 m. Deeper waters off reefs on all sediments and amongst eel-grass.	Mortensen (1940a) Taylor (1968)
<i>Centrostephanus longispinus</i>	SH	P2	P1	E. Atlantic, Mediterranean. 33-208 m. Mud, sand, gravel, coralline algae bottoms.	Koehler (1927) Mortensen (1940a) Cherbonnier (1956, 1959) Longhurst (1958)
<i>C. nitidus</i>	SH	P2	P1	Indian Ocean. 160-229 m.	Mortensen (1940a) Fell (1975)
<i>C. rodersi</i>	O	P2/3	P1	W. Pacific. 0-110 m, commonest 3-10 m. Prefer sheltered areas, living on reefs and rocky bottoms in crevices during the day. Also found on surrounding sand areas.	Tenison-Woods (1881) Bell (1884) Mortensen (1940a) H. L. Clark (1946) Sinclair (1959) Shepherd (1973) Fell (1975)



<i>Diadema mexicanum</i>	O	P2/3	P1	E. Pacific. Littoral-40 m. Coral reefs, grass and sand beds.	Chesher (1972)
<i>D. setosum</i>	O	P2	P1	Indo-Pacific. Intertidal-70 m, commonest 0-6 m. Sheltered coral reef and rock structures, and amongst corals of fringe reefs. Lives in crevices at the base of structures, moves over sediment at night. Lives unsheltered in deeper water.	Magnus (1967) Taylor (1968) James and Pearse (1969) Evans <i>et al.</i> (1973)
FAMILY MICROPYGIIDAE					
<i>Micropygia tuberculata</i>	SH	—	P1/2	Indo-W. Pacific. 150-1340 m, commonest 200-400 m. Mud and ooze bottoms.	Mortensen (1940a, b) H. L. Clark (1925a)
ORDER SALENIIOIDA					
FAMILY SALENIIDAE					
<i>Salenocidaris miliaris</i>	SH	P2	P1	Pacific. 1225-2600 m. All types of bottoms.	Agassiz (1904) Agassiz and Clark (1908)
<i>S. profundi</i>	SH	P2	P1	Tropical Atlantic. 1100-3400 m. Ooze and mud bottoms.	H. L. Clark (1925a)
ORDER PHYMOSOMATOIDA					
FAMILY STOMECHINIDAE					
<i>Stomopneustes variolaris</i>	SH	P3	P2	Indo-W. Pacific. Intertidal to immediately subtidal. Rocky shores in high energy environment. Excavates holes or lives in clefts.	Endean <i>et al.</i> (1956) Balinsky (1958) Taylor (1968, 1971)
ORDER ARBACIOIDA					
FAMILY ARBACIIDAE					
<i>Arbacia lixula</i>	SH	P4	C1	E. Atlantic, Mediterranean. Intertidal-40 m, commonest 0-5 m. On exposed steep bare rock areas. Occasionally found in crevices.	Kempf (1962) Gamble (1965) Neill and Larkum (1965)
<i>A. punctulata</i>	SH	P4	C1	W. Atlantic. Intertidal-213 m, commonest 0-10 m. Prefers rock bottoms of back reef and shore. Occasionally found on sand or shell patches. Fairly protected environments.	Harvey (1956) Sharp and Gray (1962) Kier and Grant (1965)
<i>Tetrapygus niger</i>	O	P4	C1	Peru and Chile coasts. Shore-10 m. Rocky coasts.	Mortensen (1935)
ORDER TEMNOPLEUROIDA					
FAMILY TEMNOPLEURIDAE					
<i>Amblypneustes pachistus</i>	O	P2	P2	Australia, New Zealand, 10-50 m.	Mortensen (1943a)





Species	1	2	3	Habitat	References
<b>ORDER CIDAROIDA (cont.)</b>					
<b>FAMILY CIDARIDAE (cont.)</b>					
<i>Eucidaris metularia</i>	SH	C2	C1	Indo-Pacific. Intertidal-570 m, usually very shallow. Amongst reefs, in tidal pools, in lagoons, inner and middle portion of barrier reef. Under masses of coral debris.	Mortensen (1928) Boone (1938) A. H. Clark (1950, 1952)
<i>Stylocidaris affinis</i>	O	P2	P1	Atlantic, Mediterranean. 0-1000 m, commonest 50-200 m. Coralline algae bottoms and on rock and mud bottoms.	Koehler (1927) Mortensen (1928, 1937) Cherbonnier (1956)
<b>ORDER ECHINOTHURIOIDAE</b>					
<b>FAMILY ECHINOTHURIIDAE</b>					
<i>Calveriosoma hystrix</i>	SH	P2	P1	E. Atlantic. 350-1800 m. Ooze or mud bottoms.	Farran (1913) H. L. Clark (1925b) Mortensen (1935)
<i>Hygrosoma petersi</i>	O	P2	P1	Atlantic. 200-3275 m. Mud bottom.	H. L. Clark (1925b) Madsen (1947)
<i>Phormosoma placenta</i>	SH	P1	P1	Atlantic. 215-2500 m. Mud or ooze bottoms.	H. L. Clark (1923, 1925b) Madsen (1947)
<b>ORDER DIADEMATOIDA</b>					
<b>FAMILY DIAEMATIDAE</b>					
<i>Astropyga pulvinata</i>	O	P2	P1	E. Pacific. 5-30 m. Coral reef on sand and rubble bottoms.	Mortensen (1940a) A. M. Clark (1976)
<i>A. radiata</i>	O	P2	P1	Indo-W. Pacific. 2-60 m. Deeper waters off reefs on all sediments and amongst eel-grass.	Mortensen (1940a) Taylor (1968)
<i>Centrostephanus longispinus</i>	SH	P2	P1	E. Atlantic, Mediterranean. 33-208 m. Mud, sand, gravel, coralline algae bottoms.	Koehler (1927) Mortensen (1940a) Cherbonnier (1956, 1959) Longhurst (1958)
<i>C. nitidus</i>	SH	P2	P1	Indian Ocean. 160-229 m.	Mortensen (1940a) Fell (1975)
<i>C. rogersi</i>	O	P2/3	P1	W. Pacific. 0-110 m, commonest 3-10 m. Prefer sheltered areas, living on reefs and rocky bottoms in crevices during the day. Also found on surrounding sand areas.	Tenison-Woods (1881) Bell (1884) Mortensen (1940a) H. L. Clark (1946) Sinclair (1959) Shepherd (1973) Fell (1975)
<i>Diadema mexicanum</i>	O	P2/3	P1	E. Pacific. Littoral-40 m. Coral reefs, grass and sand beds.	Chesher (1972)
<i>D. setosum</i>	O	P2	P1	Indo-Pacific. Intertidal-70 m, commonest 0-6 m. Sheltered coral reef and rock structures, and amongst corals of fringe reefs. Lives in crevices at the base of structures, moves over sediment at night. Lives unsheltered in deeper water.	Magnus (1967) Taylor (1968) James and Pearse (1969) Evans <i>et al.</i> (1973)
<b>FAMILY MICROPYGIDAE</b>					
<i>Micropyga tuberculata</i>	SH	—	P1/2	Indo-W. Pacific. 150-1340 m, commonest 200-400 m. Mud and ooze bottoms.	Mortensen (1940a, b) H. L. Clark (1925a)
<b>ORDER SALENOIDAE</b>					
<b>FAMILY SALENIIDAE</b>					
<i>Salenocidaris miliaris</i>	SH	P2	P1	Pacific. 1225-2600 m. All types of bottoms.	Agassiz (1904) Agassiz and Clark (1908)
<i>S. profunda</i>	SH	P2	P1	Tropical Atlantic. 1100-3400 m. Ooze and mud bottoms.	H. L. Clark (1925a)
<b>ORDER PHYMOSOMATOIDA</b>					
<b>FAMILY STOMECHINIDAE</b>					
<i>Stomopneustes variolaris</i>	SH	P3	P2	Indo-W. Pacific. Intertidal to immediately subtidal. Rocky shores in high energy environment. Excavates holes or lives in clefts.	Endean <i>et al.</i> (1956) Balinsky (1958) Taylor (1968, 1971)
<b>ORDER ARBACIOIDA</b>					
<b>FAMILY ARBACIIDAE</b>					
<i>Arbacia lixula</i>	SH	P4	C1	E. Atlantic, Mediterranean. Intertidal-40 m, commonest 0-5 m. On exposed steep bare rock areas. Occasionally found in crevices.	Kempf (1962) Gamble (1965) Neill and Larkum (1965)
<i>A. punctulata</i>	SH	P4	C1	W. Atlantic. Intertidal-213 m, commonest 0-10 m. Prefers rock bottoms of back reef and shore. Occasionally found on sand or shell patches. Fairly protected environments.	Harvey (1956) Sharp and Gray (1962) Kier and Grant (1965)
<i>Tetrapygnus niger</i>	O	P4	C1	Peru and Chile coasts. Shore-10 m. Rocky coasts.	Mortensen (1935)
<b>ORDER TEMNOPLEUROIDA</b>					
<b>FAMILY TEMNOPLEURIDAE</b>					
<i>Amblypneustes pachistus</i>	O	P2	P2	Australia, New Zealand, 10-50 m.	Mortensen (1943a)